STUDIES ON THE DOWNY MILDEW OF ONIONS, AND THE CAUSAL ORGANISM, PERONOSPORA DESTRUCTOR (BERK.) CASPARY[1]

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Downy mildew of the onion has been known for many years and frequently has been a subject of study. In spite of this, our knowledge of the life history of the pathogene and its environmental relations is still incomplete. The disease continues to be one of the most destructive and widespread diseases of the onion, since, for the most part, the measures recommended for its control have been impracticable and have yielded uncertain results. With heavy losses occurring in the vicinity of Elba, in western New York, during the summers of 1926 to 1929 while the writer was engaged in investigating diseases of muck crops,[2] a study of the disease and the pathogene was undertaken. The results of the investigation, together with a review of results reported by other workers, are here set forth.

NOMENCLATURE OF THE CAUSAL ORGANISM

Although the fungus causing downy mildew of onions was placed in its proper genus soon after its discovery, various specific names have been given to it. A chronological review of the taxonomy of the onion-mildew organism, and the writer's conclusions regarding the valid name, follow.

So far as is known, *Botrytis destructor* is the first name applied to the pathogene. It was published in 1841 by Berkeley, with a Latin description and an illustration of the conidial stage of the fungus. The perfect stage was not included in this description.

The name *Botrytis* (*parasitica?*) is used by Schleiden in connection with a description and a figure of the fungus in *Grundzüge der Wis-*

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senschaftlichen Botanik. There is some disagreement in regard to the date when this name was first published. Whetzel (1904) gives the third edition of Schleiden's work (1850) as the first place and date of publication; but Unger (1847), three years before the third edition was published, cited this name. Although the writer has been unable to consult the second German edition, which was published in 1845–46, the fact that this name is in the English translation of that edition but not in the first German edition, both of which have been examined, indicates that it was first published in the second German edition in 1845–46. This is probably merely a case of mistaken identification, and therefore has no standing in synonymy. The form in which Schleiden wrote the specific name (in parentheses with a question mark) and the fact that this name has already been applied by Persoon in 1796 to another fungus, occurring on the Cruciferae, indicate Schleiden's uncertainty.

Peronospora schleideni is given by Unger, with a short Latin description of the conidial stage, in 1847. Since no mention of the perfect stage is made in Unger's paper, the name is not valid according to the International Code of Nomenclature, and, furthermore, the specific name of the imperfect stage is antedated by *Botrytis destructor* Berkeley (1841).

Peronospora destructor Caspary is the name under which the fungus was listed by Berkeley in 1860, and reference was made to an earlier description of the fungus by him (1841) under the name *Botrytis destructor*. The fact that, in the generic description of Peronospora, Berkeley states that this genus possesses oospores, and explains in a footnote that this generic name was adopted because of the discovery of oospores, indicates that the perfect stage of the fungus was known at that time. The writer has been unable to determine Berkeley's reason for attributing this name to Caspary. Wilson (1914) suggested that it was probably in recognition of some manuscript name. Caspary (1855) did publish, however, a paper in which he described the discovery of oospores in *Peronospora parasitica* and other species of this genus. He puts the onion-mildew fungus in the list of those species which he says were seen either in the imperfect stage or not at all ("Species generis Peronosporae, quas vel tantum in statu manco vel non vidi"). In listing this fungus he calls it *Peronospora schleideni*. Possibly in a later paper he announced the discovery of oospores in the onion-mildew fungus, and used the new combination which Berkeley attributed to him.

De Bary used *Peronospora schleideniana* Unger in listing and describing this species in his revision of the genus Peronospora in 1863. He gave no reason for changing the form of the specific name as it was

originally published by Unger. Farlow (1884) suggested that the change was made on etymological grounds, while Gäumann (1923) said that it probably was an error on the part of de Bary.

Peronospora alliorum is the name under which this fungus was distributed by Fuckel in 1863 in Fungi rhenani exsiccati no. 41. Later Fuckel (1869) accepted the name given by de Bary and placed *Peronospora alliorum* in synonymy under *Peronospora schleideniana.*

As a result of de Bary's influence the fungus was known under the name of *Peronospora schleideniana* for many years, but recently *Peronospora schleideni* has been used more commonly.

Wilson (1914) discussed the synonymy of this fungus briefly, and considered *Peronospora destructor* (Berk.) Caspary the correct name. Gäumann (1923), however, disagreed with Wilson on this point, and insisted that the correct name is *Peronospora schleideni* Unger, since this antedates *Peronospora destructor* by thirteen years.

Gäumann was correct as far as the dates of publication of the binomials are concerned, but he evidently overlooked the fact that the species name *"destructor"* antedates *"schleideni"* by six years, and that the perfect stage is included in the description of *Peronospora destructor* while only the conidial stage is described for *Peronospora schleideni.*

The writer concludes that the valid name of the causal organism of downy mildew of onions is *Peronospora destructor* (Berkeley) Caspary, with synonymy as follows:

Botrytis destructor Berkeley, Ann. and Mag. Nat. Hist. **6**:436. 1841.
Peronospora schleideni Unger, Bot. Ztg. **5**:315. 1847.
Peronospora schleideniana (Unger) de Bary, Ann. Sci. Nat. 4:**20**:122. 1863.
Peronospora alliorum Fuckel, Fung. rhen. n. 41. 1863.

DISTRIBUTION

Downy mildew is present, and often destructive, on onions of various kinds in nearly all parts of the world. It is known to occur in Bermuda, the Canary Islands, China, Denmark, England, France, Germany, Holland, Ireland, Italy, Japan, Mauritius, New Zealand, Norway, Russia, Spain, the United States, and Western Australia. In the United States it has been reported in the *Plant Disease Reporter* (1917 to 1930) from the following States: Arkansas, California, Colorado, Connecticut, Georgia, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, New York, North Dakota, Ohio, Oregon, Pennsylvania, Vermont, Washington, West Virginia, and Wisconsin. The geographical distribution of the disease in this country, and the number of times that it has been reported from

each State, in the *Plant Disease Reporter,* are shown in figure 1. Apparently it has been observed most frequently in New York, California, Oregon, Louisiana, and Ohio. Its wide distribution, however, suggests that it may occur commonly and in other States than those

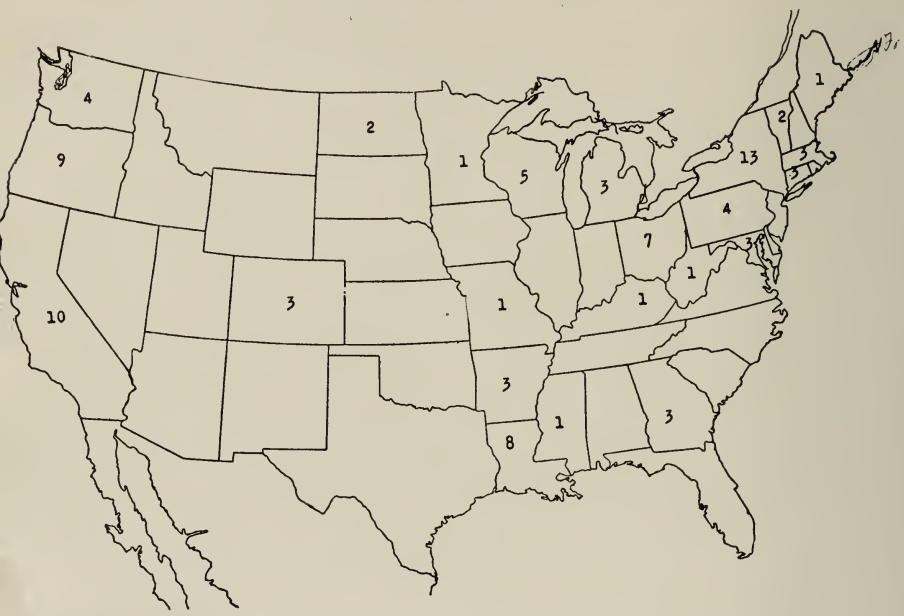

FIGURE 1. GEOGRAPHICAL DISTRIBUTION OF ONION MILDEW IN THE UNITED STATES

The numerals show the number of times that the disease has been reported in the *Plant Disease Reporter,* for each State

shown by the reports. Probably the reason why it has not been reported from more localities is that the crop or the disease is not of sufficient economic importance to attract attention.

HISTORY

The first report of onion mildew was made by Berkeley in England in 1841. Although the disease was frequently reported during the next forty-three years in Europe (Schleiden 1842, Unger 1847, de Bary 1863, Fuckel 1869, Frank 1880, and Smith 1884), it was not until the paper by Shipley (1887) appeared that a real contribution to our knowledge of the disease was made. Shipley was appointed by the British Gov-

ernment to investigate the cause of the heavy losses to the onion crop in Bermuda. He began his study by visiting the Canary Islands, where the onion seed used in Bermuda was grown, and found onion mildew to be one of the most serious onion diseases there. He made careful observations of the effect of the disease on the plants, and of the environmental conditions favoring it. In the following year he investigated the disease in Bermuda, where his earlier observations were confirmed.

Onion mildew was first reported in America by Trelease (1884). In the first annual report of the Wisconsin Agricultural Experiment Station, he devoted several pages to a discussion of the disease, which apparently was important in the Middle West at that time. Shortly afterward, Dudley (1889) found that onion mildew was destructive in New York, and Thaxter (1890) reported it on seed onions in Connecticut. L. R. Jones (1896) found it very destructive in Vermont. Whetzel (1904) gave the most complete account of the disease that had been published up to that time. No other work of consequence relating to onion mildew appeared for the next seventeen years. It is strange that such an important disease should have been so completely neglected during this period, when plant-pathological activities were expanding rapidly.

Beginning with the publication of the *Plant Disease Reporter* in 1917, there have been numerous reports of the seriousness of this disease in various parts of the country. It has been present to some extent every year, and in some years serious losses were caused by it.

More recently Murphy (1921) and Murphy and M'Kay (1926) in Ireland, Katterfeld (1926) in Russia, and Hiura (1930, a and b) in Japan, have added materially to our knowledge of onion mildew.

SUSCEPTS

Peronospora destructor appears to be confined to the genus Allium. It has been reported in literature on the following species:[3]

Allium ascalonicum Linn. (Shallot). Ritzema Bos (1898).
Allium cepa Linn. (Common onion). De Bary (1863).
Allium cepa var. *bulbellifera* Bailey (Egyptian or tree onion). Murphy and M'Kay (1926).
Allium cepa var. *multiplicans* Bailey (Potato or multiplier onion). Murphy and M'Kay (1926).
Allium fistulosum Linn. (Welsh onion). Schleiden (1842).
Allium porrum Linn. (Leek). Schöyen (1901).
Allium sativum Linn. (Garlic). Caballero (1922).

[3] The scientific names of the suscepts are taken from *The Standard Cyclopedia of Horticulture,* 1922, by L. H. Bailey.

Sorauer (1886) and Tubeuf (1895) stated that wild species of Allium are attacked by mildew, but did not give the specific names of the suscepts.

Cross-inoculation experiments were conducted, in the course of these investigations, on four species and varieties of Allium and one species of a closely related genus. The inoculum used in these experiments was obtained from *Allium cepa* var. *bulbellifera.* In all cases the plants were repeatedly inoculated under conditions favoring infection. Infection was obtained on *Allium cepa* and on *Allium schoenoprasum* Linn. So far as is known, this is the first record of the disease on *Allium schoenoprasum,* and specimens have been deposited in the herbarium of the Department of Plant Pathology at Cornell University.

Allium porrum, Allium sativum, and *Nothoscordum bivalve* Brit. (yellow false garlic) did not become diseased when inoculated, although susceptible species inoculated at the same time and under the same conditions did. Field observations failed to reveal the fungus on *Allium tricoccum* Ait. (wild leek), which grows near the onion fields at Elba. *Allium vineale* Linn. (field garlic) also failed to become infected, although it was planted in one of the experimental plots in which the disease was prevalent.

VARIETAL SUSCEPTIBILITY

Very few investigations in regard to varietal susceptibility of onions to mildew have been reported in literature. Shipley (1887) reported that both red and white varieties are attacked, but that the red varieties are the more resistant. Rosa (1926) observed that in California the seed-stalks of the white varieties are attacked earliest and most severely, and H. A. Jones (1926: 69) stated: "The foreign types like Giant Gibraltar, Sweet Spanish, Prizetaker, etc., with light green tops, appear to be somewhat more resistant than the storage varieties like Yellow Globe, Danvers, and Southport." Murphy and M'Kay (1926) reported differences in the susceptibility of the varieties under their observation. They based their conclusions on the percentage of dead plants, but stated that at the time when the counts were made practically all of the plants were diseased. Murphy and M'Kay list the nineteen varieties under their observation in the order of their resistance.

Fifty-three varieties of the common onion were grown and examined under field conditions for differences in susceptibility, in the course of this study, but practically 100 per cent of the plants became infected. Striking differences in the number of plants with dead and with living tops appeared to be due to early- or late-maturing characteristics of the varieties, rather than to the mildew. The varieties tested are listed in table 1.

TABLE 1. VARIETIES OF THE COMMON ONION TESTED FOR SUSCEPTIBILITY TO PERONOSPORA DESTRUCTOR*

1. Ailsa Craig
2. Australian Brown
3. Autumn Queen
4. Bedfordshire Champion
5. Blood Red
6. Bronze Globe
7. Ciboule Blanch Native
8. Crystal White Wax
9. Dark Red Brunswick
10. Earliest White Queen
11. Early Danvers
12. Early Large Red
13. Ebenezer
14. Extra Early Pearl
15. Extra Early Red
16. Froxfield
17. Giant Gibraltar
18. Giant Rocca
19. Golden Globe Tripoli
20. Holborn
21. Iwatsuki
22. James Long Keeping
23. Large Red Italian
24. Michigan Yellow Globe
25. Mountain Danvers
26. Mountain Red Globe
27. Natsu-negi Nebuka
28. New Mammoth Silver King
29. Nuneham Park
30. Ohio Yellow Globe
31. Pear-Shaped
32. Pearl Pickler
33. Prizetaker
34. Record
35. Red Wethersfield
36. Round Yellow Danvers
37. Rousham Park Hero
38. Senju-negi Nebuka
39. Southport Red Globe
40. Southport White Globe
41. Southport Yellow Globe
42. Straw-colored Flat Keeping
43. "The Perfect" Long Keeper
44. Tokyo Nebuka
45. Trebons
46. Up-to-Date
47. White Portuga
48. Winterheck
49. White Welsh
50. White Emperor
51. Yellow Bermuda
52. Yellow Danvers
53. Yellow Globe Danvers

* Some of these observations were made on varieties grown by E. L. Felix in testing for resistance to other diseases.

IMPORTANCE AND NATURE OF THE LOSSES

The frequent and heavy losses caused by the onion mildew have been reported by numerous writers from the time when the disease was first recorded by Berkeley (1841). Many investigators have stated that the disease causes serious damage to all stages of the common onion and other species of Allium. The actual reduction in yield is sometimes as high as 60 to 75 per cent of the normal crop.

The onion plant may be attacked and destroyed in the seedling stage, as has occurred several times in Georgia (Boyd, 1925, and Higgins, 1925). In greenhouse experiments it was found that infected onion seedlings usually died soon after the fungus fruited. Possibly some of the damping-off of the seedlings is attributable to mildew instead of to Botrytis, to which it usually is attributed.

When older plants are attacked by mildew, the bulbs are reduced in size. This fact was noted in the first written account (Berkeley, 1841), in which it was stated that the disease prevents the onions from coming to perfection. Whetzel (1904) discussed this point in considerable detail, emphasizing the fact that the fungus destroys the leaves at the time when they should be manufacturing food for the bulb, which then ceases to grow while new leaves are being developed. In turn these new leaves may be destroyed by the fungus soon after they are formed, thus further retarding the development of the bulbs. Whetzel stated that there is little or no increase in size of the bulbs following a severe attack of the fungus.

Observations by the writer also indicated that the bulbs of mildewed plants are considerably reduced in size, and an experiment was conducted in 1927 to obtain more definite information on this point. On August 4, approximately ten days after the mildew was found in the

field, the circumference of the bulbs of twelve diseased and twelve healthy plants was measured. This was accomplished without disturbing the plants, by carefully scraping a little of the soil away from the bulbs, which were already half exposed, a natural condition on muck soil. The same bulbs were measured a second time on September 1, four weeks later. Unfortunately, by that time even the plants which were healthy at the first measuring had become diseased, and so it was possible only to compare early-infected plants with those which became infected late. The results of these measurements are given in table 2.

TABLE 2. EFFECT OF DOWNY MILDEW OF ONIONS ON INCREASE IN SIZE OF THE BULBS*

Early-infected plants			Late-infected plants		
Bulb no.	Circumference in inches		Bulb no.	Circumference in inches	
	August 4	September 1		August 4	September 1
1	6.00	6.25	1	6.00	7.25
2	6.00	6.25	2	6.00	9.25
3	6.25	6.75	3	6.25	8.50
4	7.25	7.75	4	7.25	9.00
5	6.25	6.50	5	6.75	8.75
6	4.75	5.50	6	7.00	9.00
7	6.25	7.00	7	7.75	9.00
8	5.25	5.75	8	7.00	8.50
9	5.75	6.00	9	5.50	7.00
10	5.75	6.25	10	5.00	7.75
11	5.75	6.50	11	6.00	7.25
12	6.50	7.25	12†	....	....
Average	5.979	6.479	Average	6.409	8.295
Average increase in circumference 0.5±0.04			Average increase in circumference 1.886±0.14		

The increase in the circumference of the bulbs of late-infected plants over that of early-infected plants is 1.386±0.15. The odds that the difference is significant are greater than 9999 to 1.

* The probable error was calculated by Bessel's formula, P. E. $= \frac{0.6745 \times \sigma}{\sqrt{n-1}}$. This formula may not give the true probable error, since the average size of the bulbs in the late-infected group was slightly larger on August 4 than that of the early-infected group. Therefore the probable error of the first four pairs in the table, which were of the same size on August 4, was calculated according to Student's method for interpreting paired experiments described by Love and Brunson (1924). By this method the mean difference of the increase in size of the bulbs of the late-infected plants over that of the early-infected plants is 1.75 inches. The standard of deviation is 0.77, and the odds that the difference is significant are 65.2 to 1.

† This plant was missing on September 1.

The figures given in table 2 show that there is a very marked difference in the rate of growth between the bulbs of plants infected early and those of plants infected late. It is reasonable to suppose that the difference would have been even greater if the bulbs of the diseased plants had been measured earlier and the healthy ones had not become infected.

Onion mildew causes losses to the crop in storage as well as in the field. Murphy and M'Kay (1926) found that bulbs containing perennial mycelium of the onion-mildew fungus produced green shoots prematurely and then turned soft and rotted. These writers found that such losses were common in the very susceptible varieties. The present writer has noticed that in years when mildew was severe, many thick-necked onions were produced. Such onions do not cure properly, and rot in storage.

Seed plants also may be attacked. In such cases the stalks are either killed outright, causing a total loss of the seed, or they are weakened to such an extent that the seed which is formed is of inferior quality. Also, there are strong indications that the seed obtained from diseased plants may be infected or infested and thereby introduce the disease into the next crop.

FIELD OBSERVATIONS ON THE OCCURRENCE OF ONION MILDEW

SIGNS AND SYMPTOMS

The first signs of onion mildew on early-infected plants is the production of conidiophores a short distance back from the tips of the older leaves. Murphy and M'Kay (1926) considered this a sign of systemic infection. The conidiophores have a purplish tinge when fresh, and give the lesions a downy appearance. Soon the affected part of the leaf turns yellow, withers, and breaks over. Afterward the fungus may fruit at any point on the leaves with the same ultimate result, the death of the affected tissues. The writer's observations do not confirm Murphy and M'Kay's report, that the formation of the conidiophores is preceded by a pale yellowing of the affected parts of the leaves. Instead the yellowing was found to follow closely after the formation of the fungus fruiting structures.

The fungus may fruit on any part of the seed plants, but the fruiting structures usually appear first on the leaves and then on the seed-stalks. They may occur at any point on the seed-stalk from the base to the top, and occasionally are found on the inflorescence. Shortly after the fungus has fruited, the epidermal and palisade cells of the affected parts collapse and the resulting lesion becomes white, slightly sunken, and roughened. The lesions are usually circular or elliptical in shape, and involve only one side of the stalk. In some cases, however, they are large and girdle the stalk. Lesions very similar in appearance often result from mechanical injury, such as is caused by two stalks rubbing together. Such lesions have been called the "white spot disease" by Edgerton (1921), who, finding that the tissues were sterile at first, suggested that they were probably physiological in nature. In

wet weather, both the mildew lesions and those caused by mechanical injuries are soon invaded and overrun by Macrosporium. The lesions then become brownish black in color. This stage is called by Edgerton the "black stalk rot disease." The mildew lesions are so similar to the white-spot lesions that the only reliable way of distinguishing between them is by microscopical examination.

The effect of the disease on the production of seed depends on the time when infection takes place, the point at which the lesion develops, and the rate of spread of the fungus throughout the plant. Early infections usually cause greater damage than do late ones, since they weaken the plant before the seeds have had an opportunity to develop, and there is also more time for the fungus to spread throughout the plant. However, the point of attack and the nature of the lesion formed have much to do with the damage to the plant. Lesions on the lower half of the stalk, especially those that girdle it, cause the stalk to fall over, and the inflorescence, being in contact with the moist ground, may be attacked by Botrytis. Lesions that occur on the upper half and rather late in the season, however, permit seed to be formed although the stalk is completely girdled. Such lesions seldom cause the stalk to break over, and sufficient nutrients remain in the tissues above the lesions to supply the needs of the maturing seed.

The signs and symptoms of the disease on set onions and on Egyptian, or top, onions are similar to those on the seed plants and on market onions.

TIME OF OCCURRENCE

Under New York conditions, mildew may be found in the field on market onions from the middle of July to the end of the season. In 1926, at Elba, New York, the first mildewed plants were discovered on August 4. At that time, however, the wide distribution of the disease, and the advanced symptoms on many of the plants, indicated that the disease had been present for some time. In the following year more careful observations were made and the first diseased plants were found on July 23, but even then it was evident that the mildew had been overlooked for some time. During the next two years the results of the observations were similar. Although the onion fields were inspected carefully throughout the season, the first diseased plants were never found earlier than July 23, but each time evidence indicated that the mildew had been present for some time previous to its discovery. The disease is probably present to some degree from the seedling stage. Owing to the small number of diseased plants and the fact that the fungus may not fruit very abundantly because of unfavorable environmental conditions existing early in the summer, mildew spreads

very slowly at that time and is not noticed. By July or August, however, more plants have become infected, and with favorable weather conditions the disease develops and spreads very rapidly.

Mildew usually is found about two weeks earlier on set and seed plants than on market onions. In 1928 the disease was first observed by the writer on set onions on July 10, and the grower on whose farm it was found stated that it had already been present for two weeks. It was not found, however, on market onions growing in the next row until July 20. By that time it was present also on market onions in all other fields about Elba, indicating that there were sources of inoculum other than the fungus on set onions.

Mildew was found on Egyptian, or top, onions as early as the first week in July in some seasons, and was observed fruiting on them in one planting at Ithaca as late as November. The fungus seems to be perennial in these plants, and fruits whenever favorable conditions exist.

Experience has shown that a few diseased plants always can be found, even in seasons when the disease is considered to be absent. Consequently, when favorable weather conditions exist an epiphytotic may occur.

LOCATION OF DISEASED PLANTS

Each season it was observed that the disease occurred at first on individual plants which were scattered uniformly throughout the fields. Furthermore, during this early period mildew was as prevalent in fields where onions had never been grown as on old onion land. Nor did there seem to be any difference in the occurrence of the disease in fields near plantings of sets and seed onions and in fields that were isolated. After a few days of weather favoring the development and spread of the disease, the mildew became more severe on the plants next to the hedges, in low spots, where the top growth was heavy, and in other sheltered situations. It is observations on these latter stages of the disease that have given rise to the frequent erroneous statements that the disease starts in certain sheltered parts of the field and spreads to the remainder. The mildew at first is distributed uniformly throughout the field, but it spreads more rapidly in certain parts of the field than in others.

TEMPERATURE AND MOISTURE RELATIONS

Moisture was observed to have a great influence on the development and spread of the onion-mildew fungus. The formation of the fruiting bodies appears to be dependent, for the most part, on an abundance of moisture. The conidia are produced in greatest numbers during rainy periods and when the leaves are wet with dew. They are never

produced during dry periods when the leaves are entirely free from moisture. An examination of the thermograph records which were kept during the course of this investigation showed that the fungus fruits at a time of the year when the night temperatures vary between 5° and 13° C.

The effect of temperature and moisture on the viability of the conidia was even more marked. In obtaining spores for germination tests and inoculation purposes, it was found necessary to collect them early in the morning, before the dew had dried or the spores had been exposed to the direct rays of the sun. Desiccation and heat are fatal to the conidia.

With market onions it was observed that the mildew spreads most rapidly where the foliage is heavy, near hedges, in low spots, and in fields that are sheltered from the sun and wind. These conditions favor the accumulation and retention of water on the foliage of the plants, and thereby make it possible for the fungus to fruit and to infect other plants. Two seed plots on one farm, which were observed in 1927, are good illustrations of the effect of environmental conditions on the occurrence of onion mildew. One plot was located in a field that was bounded on the south by an orchard and on the west by a large barn. The planting was poorly cultivated and consequently many weeds were present. The protection thus afforded the plants prevented the rapid drying of the leaves. In this plot 85 per cent of the plants became diseased. The other plot was kept free of weeds, and, being situated on the west side of the barn, was more exposed to the prevailing winds, which favored drying of the leaves. Only 15 per cent of the plants in this field were mildewed. Another seed plot which was observed in that year was located on muck soil where the humidity was high. That also was allowed to be overgrown with weeds, and practically every onion plant became diseased.

SOURCES OF PRIMARY INOCULUM

It was deemed necessary to determine the principal sources of the primary inoculum so that methods could be developed to eliminate them and thus prevent the disease from gaining a foothold in the field. This conclusion was reached when attempts to combat the disease after it had appeared in the field resulted in failure. Even if it were possible to control the disease after it had appeared, the injury suffered by the plants from the initial attack would often be so great that they would not recover sufficiently to produce a full crop. Therefore the evidence in support of four theories as to sources of primary inoculum was considered. These possible sources were: (1) systemically infected plants; (2) infested soil; (3) infested seed; and (4) infected seed.

SYSTEMICALLY INFECTED PLANTS

Murphy (1921), Murphy and M'Kay (1926), and Katterfeld (1926) reported that a large number (approximately 45 per cent) of the onion bulbs from fields in which the disease was sevære were systemically infected with perennial mycelium of the mildew fungus. They presented evidence that this perennial mycelium is one of the principal sources of primary inoculum where onions are sown in the fall and allowed to overwinter in the field. Since this cultural practice is not followed at Elba, fall-grown onions could not be a source of primary inoculum in this section.

Perennial mycelium in onion sets, seed plants, and volunteer onions may be a source of a part of the primary inoculum in the area where these investigations were made. This is suggested by the fact that the fungus fruits on sets and seed plants several weeks in advance of its appearance on market onions. Mildewed sets and seed onions cannot be considered the main source, however, in the Elba section because there are comparatively few plantings of these on the muck, and the seedlings become diseased as early in the fields at a distance from the sets and the seed onions as in those near by. Although no volunteer onions have been observed to be infected, it is conceivable that some of them are diseased and furnish a part of the primary inoculum.

Tubeuf (1895) stated that the onion-mildew fungus occurs on wild species of Allium, but did not mention the specific names of the suscepts. The only wild species of this genus at Elba are wild leeks; and, since these were never observed to have mildew, it is very doubtful whether they are of any importance as a source of primary inoculum.

INFESTED SOIL

Oospores in the soil are probably one of the sources of primary inoculum. Although Dudley (1889), Murphy and M'Kay (1926), and many other writers on onion mildew, stated that oospores are rarely formed, Shipley (1887), L. R. Jones (1896, 1897), Whetzel (1904), Katterfeld (1926), and Hiura (1930 a) reported having found them in relatively large numbers. Jones (1897) determined experimentally that plants grown on oospore-infested soil which had overwintered became diseased, while those on clean soil did not. In spite of the lack of agreement on the importance of oospores, they have been observed in large quantities by a sufficient number of capable workers to establish their importance as a means of propagating the fungus.

Conidia are found in the soil, but, since they are very short-lived, it is unlikely that they are of importance in producing infection. Under the most favorable conditions conidia remain viable for only a

few hours, and almost certainly do not function in carrying the fungus over winter.

Mycelium in the soil is a possible, but not probable, means by which the fungus overwinters. No evidence in support of this theory is known.

INFESTED SEED

Oospore-infested onion seed may be a source of inoculum. Chapman (1910) reported the presence of spores of *Peronospora destructor* with onion seed, but did not specify whether he found oospores or conidia. Chupp (1925) states: "An examination of the seed has revealed an admixture of oospores." If this statement is based on Chapman's paper it is erroneous, since the kind of spores found was not specified. Murphy and M'Kay (1926) also assumed that Chapman meant oospores. Katterfeld (1926) found that oospores occur in the pedicels of the flowers, and Hiura (1930 a) reported that oospores are occasionally found in the flower stalks and the capsules. This being the case, it is easily understood how the oospores might become mixed with seed during the threshing process. L. D. Leach[4] stated that oospores are present in large numbers in California. This fact is especially significant, since California is the largest onion-seed-producing center in the world.

In order to determine definitely whether or not oospores do occur with the onion seed, a number of samples of commercial seed were examined by the writer. This was done by shaking a quantity of seed with about twice its volume of water, which was then poured off, centrifuged, and the sediment examined for the presence of spores. A few oospores were found in several of the samples.

The behavior of the disease at Elba suggests dissemination of the mildew fungus with the seed, since, as was shown by field observations, the disease occurred on scattered individual plants in new and isolated onion fields, which is characteristic of seed transmission. Such dissemination may occur partly by oospores mixed with the seed.

Conidia mixed with the seed are a possible, but not probable, source of primary inoculum. Since they are very sensitive to drying, they would not be able to survive storage with seed.

INFECTED SEED

A considerable amount of evidence was found in support of the theory that infected seed may be one source of primary inoculum. The distribution of the disease early in the season, which is characteristic

[4] In a letter dated August 5, 1930.

of seed transmission, has already been mentioned in the discussion of infested seed. Such distribution may also indicate infected seed. Another reason for thinking that infected seed may have a part in the spread of onion mildew is that seed plants are frequently attacked by the mildew. This was observed at Elba, New York, and onion mildew has been reported nearly every year as causing heavy losses in the onion-seed-producing sections of California.

In order to determine whether or not seed infection actually occurs, close attention was given to the plantings of seed onions. Although seed are not produced commercially at Elba, a few are grown each year by some of the growers for their own use.

The seed plots were closely observed and many flowers and seed were sectioned, but it was not until 1928 that proof of floral infection was obtained. At that time a single seed-stalk having an infected inflorescence was found. This stalk had a mildew lesion just below the flower umbel, and the fungus was fruiting sparsely on some of the flower pedicels. Microscopic examination of the conidiophores showed the fungus to be *Peronospora destructor*. Sections of the seed-stalk, the

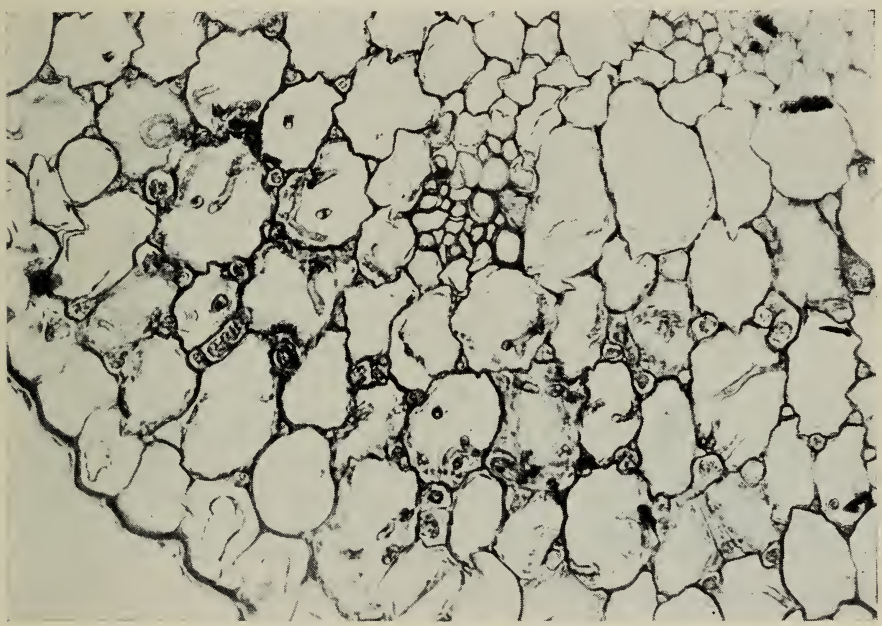

FIGURE 2. CROSS SECTION OF A PEDICEL OF AN INFECTED ONION FLOWER, SHOWING THE INTERCELLULAR HYPHAE AND THE INTRACELLULAR HAUSTORIA OF THE FUNGUS

pedicels, and the flowers, prepared at the field laboratory with a freezing microtome and stained with cotton blue in lactophenol or with one-half per cent eosin in water, demonstrated the presence of mycelium, which could be traced from the stalk up through the pedicel into the base of the ovary. In some sections conidiophores were observed arising from the mycelium in the pedicels, thus proving the identity of the fungus. The remainder of the inflorescense was fixed in chrom-acetic- and picric-acid fixing solutions, dehydrated, and embedded in paraffin for later study. Sections of this material, cut 7 microns thick and stained with Haidenhain's haematoxylin, Flemming's triple, or Delafield's haematoxylin, demonstrated the extent of the floral invasion by the mildew fungus. These sections showed that all of the flower parts had been invaded. There was an abundance of the mycelium in the pedicels (figure 2), where it consisted largely of long, straight

FIGURE 3. LONGITUDINAL SECTION OF A PETAL OF AN INFECTED ONION FLOWER, SHOWING THE LONG, STRAIGHT, INTERCELLULAR HYPHAE AND THE INTRACELLULAR HAUSTORIA OF THE FUNGUS

hyphae with numerous long and branched haustoria penetrating the cells. The mycelium itself was always intercellular, but the size and number of haustoria sometimes gave the appearance of the fungus being intracellular. The mycelium was irregular in width, depending largely on the size of the intercellular spaces through which it was passing. The fungus was easily traced from the pedicel into the receptacle, where it branched in all directions and progressed toward all of the flower organs. Long, straight hyphae ran the entire length of the petals (figure 3), and haustoria were extended into many of the cells. The mycelium was traceable from the receptacle into the stamens, where it could be followed through the filament into the anthers (figure 4). All parts of the anthers were invaded, with the exception of the pollen cavity. The mycelium was especially abundant in all parts of the ovary.

The most significant fact in relation to the mycelial invasion of the

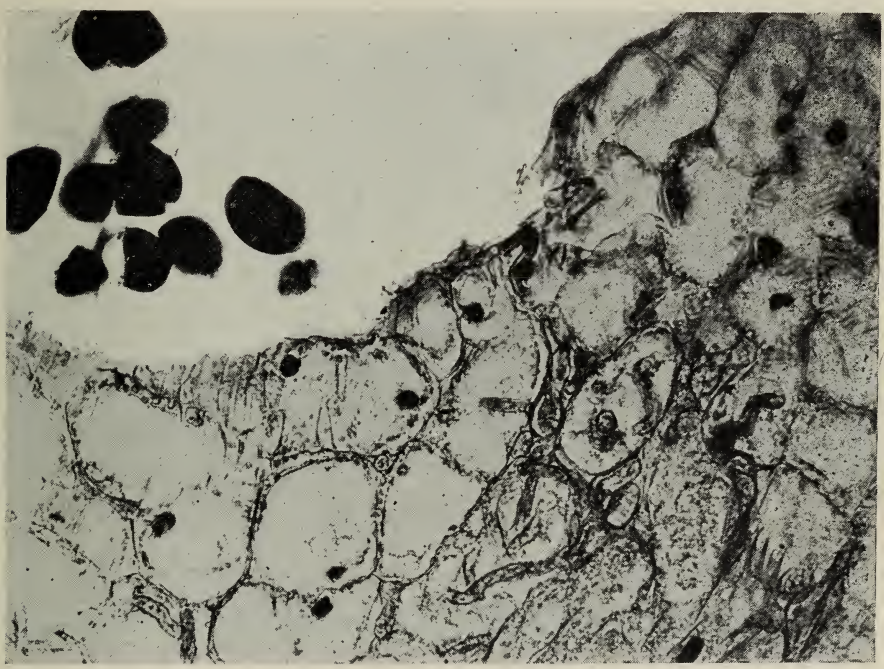

FIGURE 4. SECTION OF AN ANTHER OF AN INFECTED ONION FLOWER, SHOWING THE PRESENCE OF THE MYCELIUM OF THE FUNGUS

flower is that the fungus was present in the ovule (figures 5 and 6). A dense mat of mycelium was formed in the base of this organ (figure 6), and also was distributed entirely around the ovule. Since the only material found was immature flowers, it was impossible to determine which tissues of the mature seed would contain the fungus. Nevertheless the presence of the mycelium in such a large quantity in the base of the ovule suggests that, even though the embryo might not be invaded,

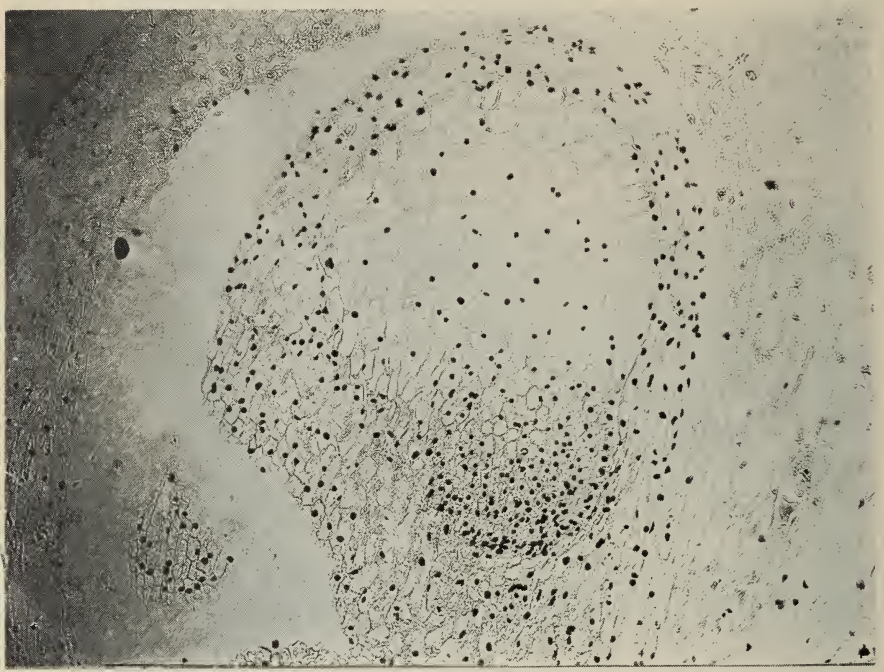

FIGURE 5. LONGITUDINAL SECTION SHOWING PART OF THE OVARY AND ONE OVULE OF AN INFECTED ONION FLOWER

the fungus would remain in the seed coat and the seedling would become infected during germination. As a rule, the seed coat of the onion remains attached to the cotyledon.

Katterfeld (1926), working in Russia, found that the mycelium almost reached the base of the ovary, but he could find none in the seed. Hiura (1930 a), working in Japan, found that the tissues of the flower stalks, and the perianths, styles, ovaries, filaments, and anthers of the

flowers, from diseased shoots contained abundant hyphae. He did not report the presence of the fungus in the ovules, however.

Katterfeld (1926), Murphy and M'Kay (1926), and Hiura (1930 a) obtained negative results in experiments on seed transmission. In the two latter investigations, seed from infected plants were planted but none of the seedlings developed the disease; while Katterfeld made a microscopic examination of the seed from diseased plants and was un-

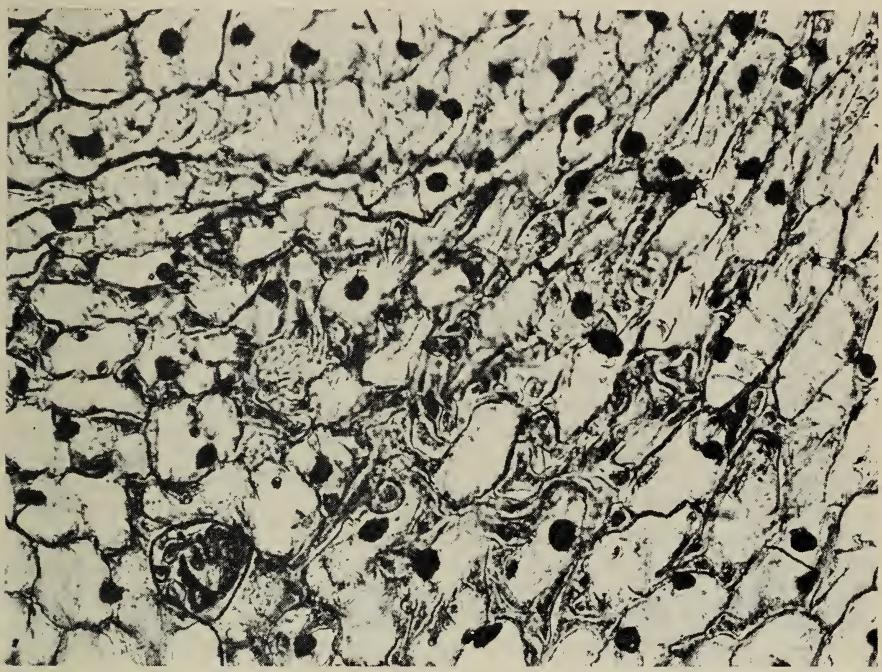

FIGURE 6. LONGITUDINAL SECTION OF AN OVULE OF AN INFECTED ONION FLOWER, SHOWING A MAT OF MYCELIUM IN THE TISSUES AT THE BASE

able to find the fungus. The results obtained by these investigators are not surprising, since it is probable that only a small proportion of seed from diseased plants is infected. Although many of the seedstalks may bear several mildew lesions, it is only rarely that the fungus is found on the flower pedicels. Even when it is found fruiting on some of the flower pedicels, usually others in the same umbel are not invaded. It is probable also that only a small number of the invaded flowers mature viable seed.

Since obtaining the above evidence that *Peronospora destructor* may be transmitted in the seed, a review of the literature and further work with other downy mildews has shown that seed transmission of members of the Peronosporales is probably of frequent occurrence and is one of the principal means by which they overwinter and are disseminated. Although seed transmission of *Phytophthora phaseoli* has not been actually demonstrated, the work of Clinton (1906) has shown that it probably does occur. Angell (1929) gives relatively conclusive experimental evidence that the organism causing blue mold of tobacco is carried in or with the seed. The manner in which this disease made its first appearance in this country would indicate also that the inoculum was widely distributed and needed only the proper environmental conditions for its development. Wolf and Lehman (1924), in their studies on downy mildew of soybean, found circumstantial evidence that *Peronospora manshurica* is transmitted with the seed. Leach (1931) found mycelium and oospores of *Peronospora schachtii* in the sepals, pericarp, filaments, and ovules of beet flowers, but was unable to find them in the nucellus and the embryo. By controlled germination tests, however, he was able to obtain evidence of seed transmission of the beet-downy-mildew fungus. According to the *Plant Disease Reporter,* beet mildew is as severe on beet seed-plants in California as is onion mildew on onion seed-plants. Eriksson (1925) also cites evidence of seed transmission of beet mildew. The writer's own observations on the downy mildews of spinach, crucifers, and cucurbits point to seed transmission of the causal organisms of these diseases. It has been observed frequently that cucumbers are attacked by mildew as early and as severely when grown on new and isolated fields as when grown on old land or near other fields of cucumbers. *Peronospora parasitica* frequently was found fruiting on the seed pods of kale and cabbage, and it is probable that the fungus enters some of the seed. Observations have shown that *Peronospora effusa* is present on practically all spinach seed-plants, and that it fruits on some of the seed. Sections of these seed have demonstrated the presence of the fungus in the ovary and in the seed coat. The seed of commerce consists of the ovule surrounded by the ovary.

ENVIRONMENTAL FACTORS

FIELD OBSERVATIONS

In studying onion mildew in the field, an attempt was made to determine the climatic conditions favoring the development and spread of the disease. However, with so many variable factors only general conclusions could be reached. It was observed that, as a rule, mildew was not found until late July or early August, when the nights were

relatively cool and heavy dews occurred frequently. Prolonged rainy and muggy periods also were very favorable for the development and spread of the disease. The fungus was found capable of producing conidiophores and conidia at rather low temperatures. The fresh fruiting structures were found on numerous occasions at Elba during the latter part of September, when the night temperature was as low as 5° C. Conidia were found also on Egyptian onions as late as the middle of November in 1929 at Ithaca.

EXPERIMENTAL WORK

Relation of temperature to the formation of conidiophores and conidia

Experiments on the relation of temperature to the formation of conidia were not conducted in carefully controlled chambers. However, a few tests were made on this phase of the problem in the greenhouse and the laboratory. The results of these tests are presented here, since they show the approximate temperature range over which conidia may be formed.

Infected plants were placed at four different temperatures in the greenhouse. One test was sufficient to show that the fungus would fruit at all temperatures tested (10° to 28° C.). Following this test, two infected plants were brought into the laboratory, sprayed with water, and treated as follows: one was placed in a 3°-C. incubator under a bell glass to prevent evaporation of the water, while the other was placed under a bell glass in a room where the temperature rose as high as 34° C. during the night. The next morning fruiting structures were found on both plants. There is no question about the conidia having been formed at 3° C., because the temperature remained constant in the incubator. It is possible, however, that 34° C. is too high a temperature for the formation of conidia, and that in this case they were formed before the temperature rose to that degree. Murphy and M'Kay (1926) found that conidiophores were first produced when the maximum temperature was 10° C., but that they were much more abundant several days later, when it rose to 23°. Katterfeld (1926) found that they were formed at 9.5° to 11° C. These workers did not report the determination of the full range of temperature over which conidiophores are formed. Hiura (1930 b) found that the optimum temperature for the production of conidia was near 15° C., the minimum was 6°, and the maximum was 25°.

Relation of humidity to the formation of conidiophores and conidia

As stated above, preliminary observations and experiments in the field and the greenhouse indicated that an abundance of moisture is necessary for the formation of conidiophores. In order to determine

definitely the hygroscopic requirements of the fungus for fruiting, a series of experiments was run at the New York State Agricultural Experiment Station at Geneva, where a chamber in which the humidity could be controlled was made available through the kindness of Dr. J. G. Horsfall. The plants used in these experiments were inoculated in the greenhouse at Ithaca and were taken to Geneva after the period of incubation had passed. Accident reduced the number of plants that could be used successfully in the first experiments, but the test was repeated later for the writer by Dr. Horsfall with a different set of inoculated plants.

The experiments were conducted at night, since humidities could not be maintained in the chambers under conditions existing during the day.

The following plan of experiment was adopted. As many plants as the chamber would hold were thoroughly watered and placed in the chamber late in the afternoon. Some of these were atomized with water and covered with bell glasses to make sure that the water would remain on the leaves all night. The hydrostat was set for as near 100 per cent humidity as was possible. A hygrothermograph placed in a box gave a complete record of the temperature and humidity, and a sling psychrometer placed where it would be exposed to the current of air set up by a fan furnished an additional check on the temperature and humidity.

The plants under the bell glasses were in an atmosphere of 100 per cent humidity with water on the leaves, while the others were in an atmosphere of slightly lower humidity and without visible water on the leaves. Plants that did not produce conidia under the conditions of the experiments were afterward tested to make sure that they were infected. This was accomplished by spraying the plants with water and placing them under bell glasses on the greenhouse bench or in a chamber with high humidity. Only those that were proved to have been infected are included in the experimental results.

The plan of the second experiment was changed on February 21. On that date the plants under the bell glasses were not watered, and so their leaves remained dry, while those in the humidity chamber were sprayed continually with water.

The results of the experiment on humidity are shown in table 3. An examination of this table shows that twenty-one of the twenty-two plants produced conidia when they were exposed to high humidities (98 to 100 per cent) and when there was visible water present on the leaves; thirteen of these twenty-one had previously failed to produce conidia when exposed to high humidities but without water on their leaves. The results of these tests indicate that water must actually be present on the leaves for conidiophores and conidia to be formed. Two of the twenty-two plants formed conidiophores and conidia when

TABLE 3. RELATION OF HUMIDITY TO THE FORMATION OF CONIDIOPHORES AND CONIDIA

Plant no.	Date	Treatment	Relative humidity (per cent)	Leaves wet or dry	Conidia present or absent
		First series of tests			
1	Dec. 1	Humidity chamber	100	Wet	+
8	Dec. 1	Humidity chamber	100	Wet	+
25	Dec. 1	Humidity chamber	100	Wet	+
55	Dec. 5	Humidity chamber	99	Dry	–
55	Dec. 6	Inoculation chamber	100	Wet	+
66	Dec. 4	Humidity chamber (B. G.)*	100	Wet	+
67	Dec. 6	Humidity chamber	98	Dry	–
67	Dec. 7	Inoculation chamber	100	Wet	+
69	Dec. 4	Humidity chamber	98	Dry	–
69	Dec. 5	Bell glass on bench	100	Wet	+
51	Dec. 6	Humidity chamber	99	Dry	–
51	Dec. 7	Inoculation chamber	100	Wet	+
34	Dec. 6	Humidity chamber (B. G.)	100	Dry	–
34	Dec. 7	Inoculation chamber	100	Wet	+
40	Dec. 6	Humidity chamber	99	Dry	–
40	Dec. 7	Inoculation chamber	100	Wet	+
81	Dec. 4	Humidity chamber	98	Dry	–
81	Dec. 7	Inoculation chamber	100	Wet	+
73	Dec. 4	Humidity chamber	98	Dry	–
73	Dec. 7	Inoculation chamber	100	Wet	+
50	Dec. 6	Humidity chamber	99	Dry	–
50	Dec. 7	Inoculation chamber	100	Wet	+
		Second series of tests			
10	Feb. 19	Humidity chamber	99	Dry	–
10	Feb. 21	Humidity chamber (B. G.)	100	Dry	+
12	Feb. 19	Humidity chamber	99	Dry	–
12	Feb. 21	Humidity chamber	100	Wet	+
23	Feb. 19	Humidity chamber	99	Dry	–
23	Feb. 21	Humidity chamber	100	Wet	+
29	Feb. 19	Humidity chamber	99	Dry	–
29	Feb. 20	Humidity chamber (B. G.)	100	Wet	+
29	Feb. 21	Humidity chamber	100	Wet	+
30	Feb. 19	Humidity chamber	99	Dry	–
30	Feb. 20	Humidity chamber (B. G.)	100	Wet	+
75	Feb. 19	Humidity chamber (B. G.)	100	Wet	+
75	Feb. 21	Humidity chamber (B. G.)	100	Dry	+
81	Feb. 19	Humidity chamber (B. G.)	100	Wet	+
81	Feb. 20	Humidity chamber (B. G.)	100	Wet	+
81	Feb. 21	Humidity chamber (B. G.)	100	Wet	+
83	Feb. 19	Humidity chamber	100	Wet	+
89	Feb. 19	Humidity chamber (B. G.)	100	Wet	+
89	Feb. 21	Humidity chamber	100	Wet	+
92	Feb. 20	Humidity chamber (B. G.)	100	Wet	+
92	Feb. 21	Humidity chamber (B. G.)	100	Wet	+

* " B. G.", plants covered with a bell glass.

exposed to high humidities without water on their leaves. This was probably because sufficient water had accumulated at the stomata during transpiration in the humid atmosphere to allow the formation of the fruiting structures. It is possible that conidia would always be formed in an atmosphere of 100 per cent humidity, provided that sufficient time were allowed for water to accumulate around the stomata.

These tests supported the conclusions reached from field observations and greenhouse practices. In the field it was always noted that the fungus fruited only when water was present on the leaves in the form of rain or dew, and in the greenhouse the diseased plants were always sprayed with water and covered with a bell glass to obtain conidia. On a number of occasions a few conidia were formed on plants in the greenhouse which had not been sprayed with water and covered with bell glasses. This occurred only at times when the humidity was very high, and water had probably accumulated around the stomata during transpiration as occurred in two of the plants included in table 3.

SPORE GERMINATION

Preliminary studies on spore germination made at the field laboratory indicated that in order to obtain good germination it was necessary to control the environmental factors as well as to have fresh spores. The introduction of the fungus into the greenhouse at Cornell University in the fall of 1929 made possible further studies on germination.

TECHNIC

Fresh spores for use in these tests were obtained by spraying an infected plant in the greenhouse with water and placing it under a bell glass for the night. On the following morning the fresh conidia that had been formed during the night were brought into suspension by dipping the mildewed leaves into water. In this manner only fresh mature spores were obtained, and they were protected from desiccation since they were not exposed for any length of time to the air. Drops of the suspension were placed on clean microscope slides in moist chambers and these were placed in incubators at different temperatures. The necessary apparatus for the tests was placed in the incubators the night before, so that it would be at the temperature at which the spores were to be tested.

Distilled water was used at first as a suspension medium for the spores, but, since many of the spores were ruptured owing to high osmotic pressure, it was necessary to find a more favorable medium. A test in which the germination of the spores in distilled water, in lake water, and in physiological salt solution, was compared, showed lake water to be a suitable medium. The results of the test are given in table 4.

This test showed that lake water and physiological salt solution were more favorable media than distilled water for spore-germination tests because they were more nearly isotonic with the spore contents. Since the best germination was obtained in lake water, this was used in all the subsequent preparations of spore suspensions. In all cases the water was collected in Erlenmeyer flasks, and was sterilized before being used in order to prevent the development of bacteria and algae.

TABLE 4. EFFECT OF SUSPENSION MEDIUM ON SPORE GERMINATION

Suspension medium	At 12° C.		At 15° C.	
	Per cent germinated	Per cent ruptured	Per cent germinated	Per cent ruptured
Distilled water	46	38	18	51
Lake water	75	4	74	7
Physiological salt solution *	65	0	31	2

* The physiological salt solution was an 0.85-per-cent solution of sodium chloride in distilled water.

EFFECT OF TEMPERATURE ON THE TIME AND THE PERCENTAGE OF GERMINATION OF THE CONIDIA

After the above preliminary tests had been completed, germination experiments were conducted at the following temperatures: 3°, 6°, 11°, 13°, 18°, 21°, 27°, 30°, and 35° C. The spores used in these tests were prepared as described above. Six slides, each slide bearing three drops of spore suspension, were used for each temperature. One slide for

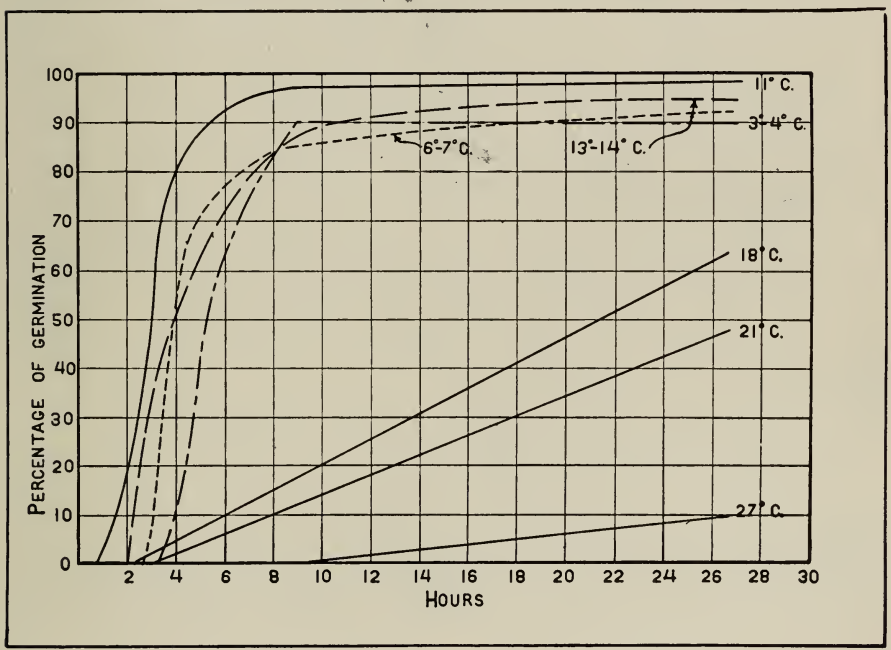

FIGURE 7. EFFECT OF TEMPERATURE ON THE TIME AND THE PERCENTAGE OF GERMINATION OF CONIDIA OF PERONOSPORA DESTRUCTOR

each temperature was examined at the end of two, three, four, five, seven, and twenty-four hours, respectively, and the percentage of germination in each drop was noted. The percentage of germination was obtained by counting 100 spores in each drop. The results, presented in figure 7, are based on three replications and on counts of approximately 5500 spores for each temperature tested.

According to these results the optimum temperature for germination of these spores is 11° C., since at this temperature germination was the most rapid and complete. Within six hours approximately all of the spores had germinated. Spores kept at lower temperatures germinated slightly more slowly, but the final percentage of germination was nearly as high. Those kept at 13° to 14° behaved similarly. At 18° and above, the higher the temperature, the lower was the final percentage of germination. No germination occurred above 27°.

Temperature also had an effect on the type of germ tube formed.

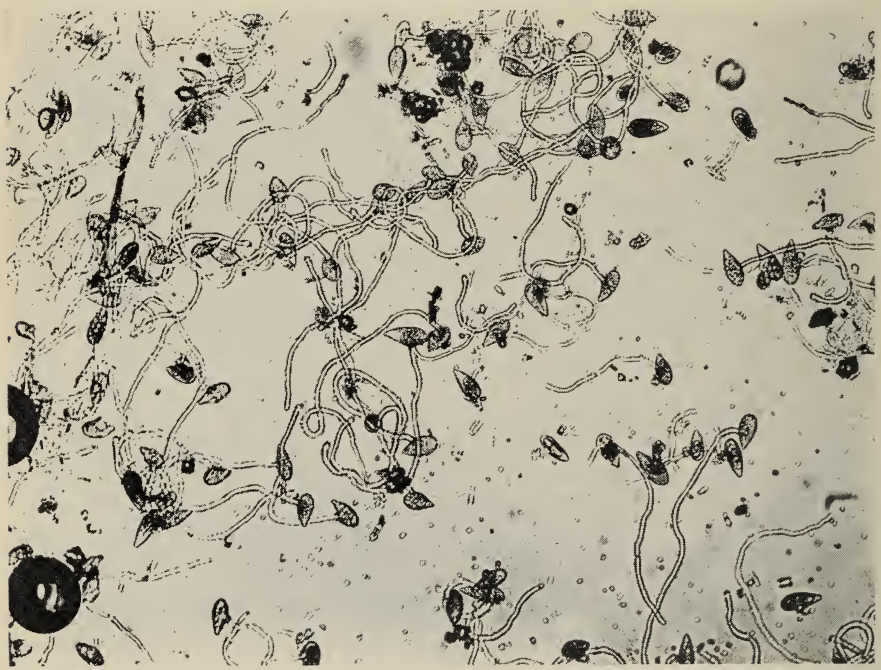

FIGURE 8. GERMINATION OF CONIDIA OF PERONOSPORA DESTRUCTOR AT THE OPTIMUM TEMPERATURE

Germ tubes developed at or near the optimum temperature for germination were the longest and appeared to be the most nearly normal in shape (figure 8). Those produced at the high temperatures were short and tended to be misshapen (figure 9), while those at the low temperatures were longer than those at the high temperatures but shorter

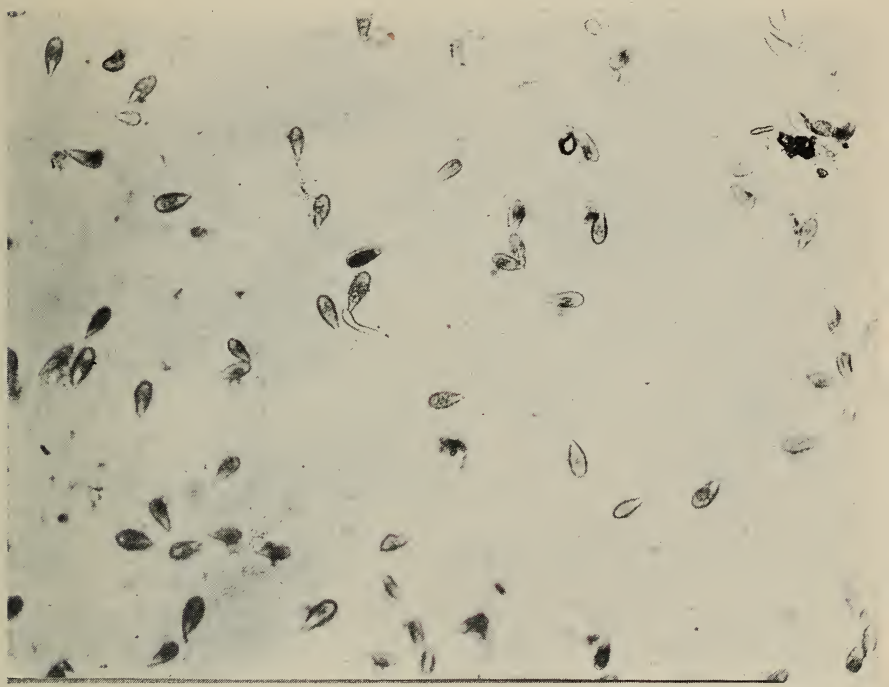

FIGURE 9. GERMINATION OF CONIDIA OF PERONOSPORA DESTRUCTOR AT HIGH TEMPERATURES

than those at the optimum. The peculiar type of germ tube produced at low temperatures is illustrated in figure 10.

Normal germination is by a single germ tube, or occasionally two tubes, produced from the side of the conidium. Less frequently, a single germ tube may be produced from the apical end of the spore. The germ tubes are uniform in diameter, measuring from 5.76 to 7.68 microns, and have been observed to attain a length of 940 microns. As a rule they remain unbranched, but occasionally they undergo branching. The latter condition is found at times in rain water, in

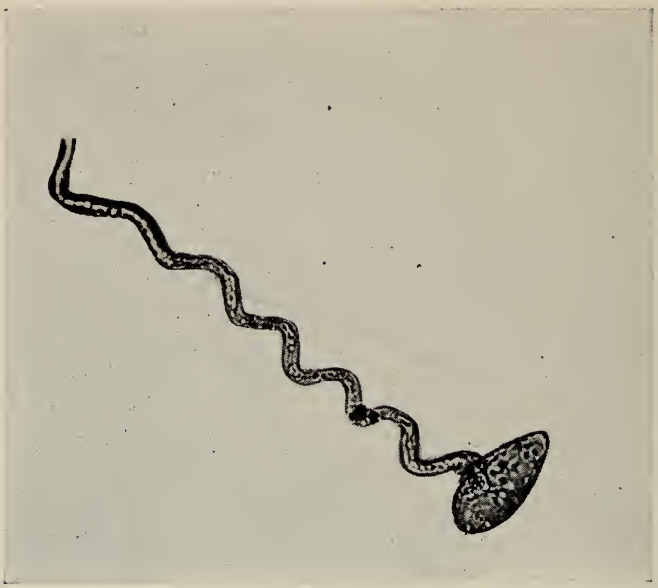

FIGURE 10. GERMINATION OF CONIDIA OF PERONOSPORA DESTRUCTOR AT LOW TEMPERATURES

dew collected from onion leaves, and in Knop's nutrient solution (figure 11).

Murphy and M'Kay (1926) obtained germination at 8.5 to 10° C., a trace at 25°, and none at 30°. They do not report temperatures lower than 8.5° C., nor apparently did they determine the exact optimum temperature. Katterfeld (1926) studied the germination in considerable detail, paying especial attention to the rate of growth of the germ tubes, the rate of germination, and the ability of the conidia to germinate. His tests were run at a laboratory temperature of 10° to 12° R. (12.5° to 15° C.) and 14° R. (17.5° C.), which, according to the writer's experiments, are favorable temperatures for germination although a little higher than the optimum. By making observations every one and one-half hours Katterfeld found that at a temperature of 15° C. the rate of growth of the germ tubes during the first five and one-half hours varied from 46 to 111 microns and averaged 101 microns per hour. Although the writer did not make a special study of the rate of growth, his observations in general confirm Katterfeld's in that the

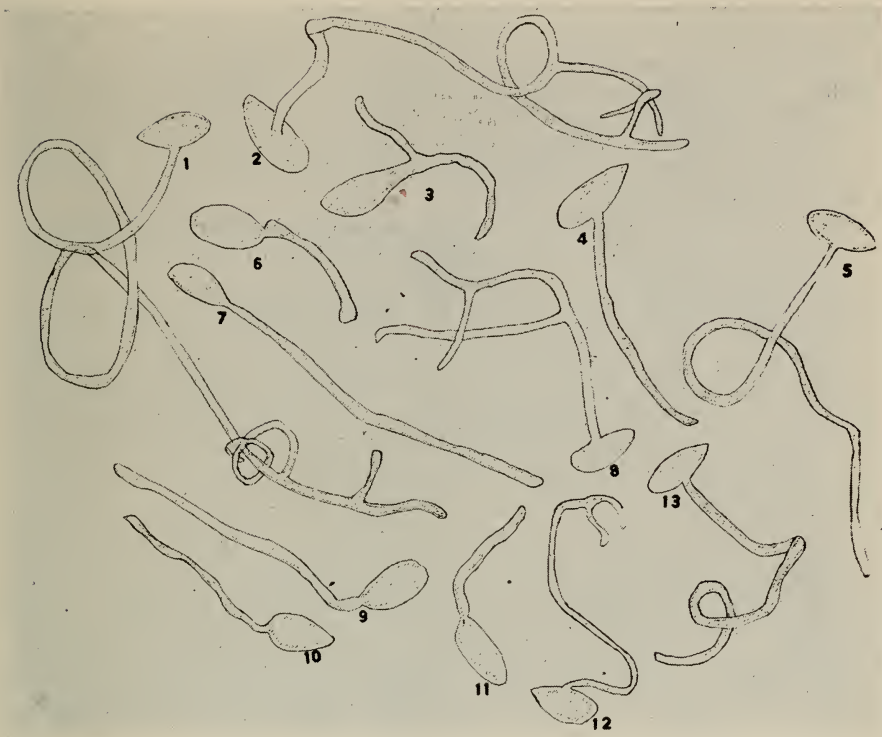

FIGURE 11. VARIOUS TYPES OF GERMINATION OF THE CONIDIA OF PERONOSPORA DESTRUCTOR

germ tubes were found to grow very rapidly and the growth rate increased with the increase in temperature up to about 21° C. In studying the rate of germination, Katterfeld found that, where he obtained a germination of 100 per cent, from 64 to 100 per cent of the spores germinated between two and two and one-half hours after being sown, and that the rate was lower when the total germination was lower. He found that all viable conidia germinated in five hours. These results differ from those presented in figure 7, in that at the optimum temperature only 50 to 60 per cent of the conidia had germinated by the end of the first two and one-half hours and complete germination was not accomplished for about twenty-four hours.

Katterfeld found that conidia capable of germination could be readily recognized by their appearance. The viable conidia refracted light, had tense walls, and were completely filled with protoplasm. Loss of vital-

ity was shown by a loss of tension and a withdrawal of the cytoplasm from the walls. Katterfeld found that immature conidia were capable of germination but produced shorter germ tubes than did mature conidia. Conidia exposed to an atmosphere of 100 per cent humidity lost their germinating power after fifteen to seventeen hours, while those exposed to dry laboratory air were not able to germinate after one and one-half to two hours. The writer is in agreement with Katterfeld on these points.

Hiura (1930 b) found that the time required for the germination of conidia varies with the temperature and with the conidia. His conclusions in regard to the optimum, minimum, and maximum temperatures for conidial germination are approximately the same as those of the writer. He found the optimum to be near 10° C., the maximum near 20°, and the minimum below 5°. His results regarding the time required for germination do not agree wholly with those obtained in this study, however. According to Hiura's results, the time required for germination decreases up to the optimum temperature, but does not increase appreciably above the optimum as was shown by the writer's results.

INFECTION

Infection is dependent on an abundance of viable conidia and environmental conditions favoring their rapid germination. In practice it was found that by applying the information obtained in the experiments on the relation of temperature and moisture to spore formation and germination, infection could always be obtained. Infection was determined by the production of conidia when the plants were placed under favorable conditions for their development.

Spores were obtained for inoculation as described under *Technic* (page 26), and were immediately taken to the laboratory. Here potted plants were sprayed thoroughly with the spore suspension and were then placed under moist bell glasses in the incubators at temperatures below 18° C. for twelve to twenty-four hours. The plants were then removed to the greenhouse, where they were kept in a cool room with a maximum temperature of approximately 20° C. and a minimum temperature of about 10°. Plants inoculated in this manner always became infected; but infection seldom took place when the inoculum had been exposed to dry air or to high temperatures, or when the plants were not kept cool for at least twelve hours after inoculation.

INCUBATION PERIOD

The incubation period was determined by inoculating a group of potted plants under favorable conditions, as described above, and then

testing for infection by placing moist bell glasses over the plants. In order to avoid injury by Botrytis, the plants were divided into two groups and these groups were tested on alternate days by covering with bell glasses. In this manner neither group was exposed continuously to a humid atmosphere. The temperature of the greenhouse in which these tests were conducted was from 10° to 24° C. The results obtained in two of these tests are shown in table 5.

TABLE 5. INCUBATION PERIOD OF PERONOSPORA DESTRUCTOR IN ALLIUM CEPA

Number of plants	Number of days between inoculation and the production of conidia
3	11
3	12
2	13
2	14
1	15

From these results it is seen that the incubation period is from eleven to fifteen days under the conditions of this experiment. Of twenty-three other plants that were placed under bell glasses between thirteen and twenty days after inoculation, twenty-two produced conidia, indicating that the incubation period had already been completed. These results agree with those of Katterfeld (1926), who found the incubation period to be ten to fifteen days in the greenhouse and thirteen to eighteen days in the garden. They differ from those of Murphy and M'Kay (1926), who found the period to be twenty-three days.

EFFECT OF TEMPERATURE ON INFECTION

Eight plants were inoculated under favorable conditions for infection on January 25, and on the following day they were transferred to the greenhouse, where half of them were placed in a warm room (19° to 33° C.) and the other half in a cool room (10° to 24° C.). Beginning six days after inoculation, half of the plants in each house were tested for conidial production every other day by placing them under bell glasses after spraying them with water. The results of these tests are shown in table 6.

This experiment indicated that high temperatures are unfavorable for the development of the fungus in the host tissues. Even though all of the plants were inoculated and treated alike during the first twenty-four hours, none of those kept at the warm temperature developed conidia although all four of those kept in the cool house produced them in eleven to sixteen days after inoculation. The tests

TABLE 6. EFFECT OF TEMPERATURE ON INFECTION OF ONIONS BY PERONOSPORA DESTRUCTOR*

Number of days after inoculation	Warm house				Cool house			
	Plant no.				Plant no.			
	94	95	96	97	98	99	100	101
6	.....	.....	.....	.....	.....	.....	.....	.....
7	−	−	.....	.....	−	−	.....	.....
8	.....	.....	−	−	.....	.....	−	−
9	.....	.....	.....	.....	.....	.....	.....	.....
10	−	−	.....	.....	−	−	.....	.....
11	.....	.....	−	−	.....	.....	−	+
12	−	−	.....	.....	−	+	.....	.....
13	.....	.....	−	−	.....	.....	+	+
14	−	−	.....	.....	+	+	.....	.....
15	.....	.....	.....	.....	.....	.....	.....	+
16 †	.....	−	.....	.....	+	.....	.....	.....

* The minus and plus signs in the body of the table indicate the absence or the presence of conidial formation following a test for infection.
† The experiment was continued through twenty-nine days without further results.

were discontinued after the twenty-ninth day, since by that time none of the plants in the warm house had produced conidia. It is possible that the fungus may have been killed by the high temperature in the warm house.

CONTROL

The field application of fungicides which was formerly recommended for the control of onion mildew was found during the investigation to be unpractical, costly, and of doubtful value. It is unpractical to spray or dust with the usual mixtures now available, because the waxy covering of the leaves prevents the materials from adhering; and the thick top growth makes it very difficult, at least, to spray or dust without causing serious injury to the plants. In order to protect the plant properly, it would be necessary to begin spraying or dusting in the seedling stage and to continue the treatment until shortly before harvest. This would make the cost of growing onions prohibitive. Spraying with 4–4–50 bordeaux mixture and dusting with 20–80 copper-lime dust and Kolodust, in the course of this study, failed to give any indication of controlling the disease.

A more practical and beneficial means of control is considered to be the exclusion of the fungus from new land or from fields that have not been used for onions for several years. Sanitation, rotation, and avoidance of the environmental conditions favorable for the spread of mildew, are additional measures to be recommended.

It may be possible to accomplish the first of these measures by using only disease-free seed and sets, and by avoiding the introduction of

soil from infested fields on tools and on transplants. It is possible that disease-free seed may be procured from sections of the country in which onion mildew does not occur, or perhaps it can be grown from disease-free seed bulbs. Such bulbs may be obtained by selection or by treating with hot air at 40° C. for eight hours. Murphy and M'Kay (1926) found that this treatment would kill the fungus in the bulb. Disease-free sets also may be obtained in this manner.

Sanitation and rotation will aid in reducing the amount of inoculum in the soil. The onion refuse consists largely of tops which may contain oospores and of culls which may be systemically infected. Practically 100 per cent of the onion refuse was burned at Elba in the fall of 1927, 1928, and 1929 for the control of onion maggots. This practice was accompanied by a decrease in the severity of onion mildew during those years. At present the length of time that the fungus will remain viable in the soil is not known, and so the length of rotation necessary for the elimination of the fungus from the soil is uncertain.

The severity of the disease can be reduced to some extent by regulating the environmental conditions. The location of the onion field has much to do with prevalence of the disease. As a rule, onions grown in fields that are well drained and are exposed to the sun and wind suffer less from mildew than do those in fields on low ground or surrounded by high windbreaks. Furthermore, no work should be done in the onion fields while the leaves are wet with dew or rain, because the spores are viable under such conditions and may be carried on the clothing of the workmen to other plants in the field.

SUMMARY

Downy mildew, caused by *Peronospora destructor* (Berk.) Caspary, is one of the most serious diseases of the onion crop.

Evidence has been presented to show that *Peronospora destructor* (Berk.) Caspary is the valid name of the causal fungus.

The disease is widely distributed, occurring in nearly all parts of the world and in most of the principal onion-growing sections of the United States.

A brief history and review of the literature of onion mildew is given.

Peronospora destructor has previously been recorded on seven species and varieties of Allium. *Allium schoenoprasum* is here recorded as a new suscept. Fifty-three varieties of the common onion were tested and found to be equally susceptible to onion mildew.

Losses may be sustained at any stage in the life of the plant. Data are presented to show that the bulbs are considerably stunted by the disease.

Field observations were made on the occurrence of the disease on market onions, set onions, seed onions, and Egyptian onions. The disease was found to be favored by abundant moisture and relatively low temperatures. Market onions were found to become diseased as early and as frequently on new as on old land. The first diseased plants were found to be scattered throughout the fields.

There are four sources of primary inoculum: systemically infected plants, infested soil, infested seed, and infected seed. Evidence presented points to the fact that mycelium in the seed is an important source of primary inoculum.

The fungus was found to fruit over a wide range of temperatures. Water on the leaves was necessary for the formation of conidiophores and conidia.

Lake water was found to be the most satisfactory medium tested for spore germination. The optimum temperature for spore germination was found to be 11° C., but the full range over which the spores germinate was 3° to 27° C.

An abundance of moisture, and low temperatures, were found necessary for infection. The incubation period was about eleven to fifteen days.

Fungicidal treatment is not considered a satisfactory method of control. Exclusion of the fungus from new areas, sanitation, and regulation of the environmental conditions, are considered the most promising means of combating the disease.

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